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Anatomical and morphological studies of seed development in *Sandersonia aurantiaca* (Hook.)

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Seed development, including the development of the embryo, the endosperm and the seed coat of *Sandersonia aurantiaca* (Hook.) has been studied. Seed development in *S. aurantiaca* takes about 60 days from pollination to maturity. The embryo passes through the early globular, the late globular and the elongated spheroidal stages before reaching the linear embryo stage. Endosperm development conforms to the nuclear type. The cellularisation of the endosperm starts at about 14 days after pollination (DAP) when the embryo reaches the early globular stage, and terminates at about 21 DAP when the embryo is in the late globular stage. The mature seed is globose with a strophiole around the micropyle. The embryo is linear and shows a prominent radicle, a small embryonic axis, shoot apex and large cotyledon. The endosperm constitutes most of the seed volume and contains cells with thickened walls and many storage bodies. The seed coat of a mature seed differentiates into three layers: the epidermis, the subepidermal parenchyma (middle layer), and the lignified layer. Both epidermis and subepidermis come from the outer integument. The lignified layer is derived from both the outer and inner, or only the inner integument.

Introduction

Sandersonia aurantiaca Hook. (Colchicaceae) is a deciduous monocotyledonous perennial herb, related to *Gloriosa* and *Littonia*. It is a tuberous plant with clear orange flowers and occurs naturally in South Africa (Natal and Cape provinces) at an altitude of 600–2 000m in areas of high summer and low winter rainfall (Mathew 1978, Brundell and Reyngoud 1985). The bright orange flowers with their distinct shape and good vase life have made *Sandersonia* a sought-after cut flower on the international market (Eason and Webster 1995).

In *Sandersonia* the flowers are axillary in the upper part of the stem and are borne on slender pedicels 2–3cm long (Mathew 1978). The six tepals are fused together to form an inflated urn-shaped, pendulous, bright orange perianth, 2–2.5cm long, with six prominent spurs on the base (Mathew 1978). The tips of the segments are just free and curl outward. Sterling (1975) studied the morphology of the carpel in *Sandersonia* and indicated that the pistils were generally tricarpellate and had many ovules. He reported that the ovules were mostly plagiotropic, anatropous and essentially bitegmic, with inner integuments often nearly fused with nucellar remnants. The ovules in some specimens showed a small obturator (a funicular proliferation in the form of a protuberance which brings the stigmatoid or transmitting tissue into close proximity to the micropyle).

Flower buds of *Sandersonia* are visible 3 weeks after planting the tubers, with numbers of buds increasing until week 6, and flowers opening between weeks 7 and 9 (Brundell and Reyngoud 1985). The dry weight of the flowers continues to increase until week 11, then declines. The development and senescence of *Sandersonia* flowers have been described by Eason and Webster (1995). They assigned twelve stages of development and senescence according to flower size, shape, a reduction of fresh weight and of soluble protein, loss of pigment, wilting and necrosis of the tepals.

The present investigation was undertaken to provide a detailed account of seed development in *Sandersonia*. The purpose of the study is to investigate the development of the embryo, the endosperm and the seed coat of this species.

Materials and Methods

Sandersonia plants obtained as tubers from commercial sources were grown in a glasshouse with a ventilation temperature of 25°C and a heating temperature of 15°C. Seed production was ensured by hand pollinating flowers. Flowers for analysis were collected on day 0 (the day before pollination), 1, 4, 5, 6, 7, 8, 9, 10, 12, 14, 21, 28, 35, 42, 49, 56 days after pollination (DAP) and a final full-maturity stage. On

days 0, 1, 8, 14, 21, 28, 35, 42, and 56, samples of the harvested flowers were dissected and ovule diameters measured.

The materials studied for seed development were fixed in a mixture of 4% formalin, glacial acetic acid and 70% ethyl alcohol (FAA) in proportions 5:5:90 at younger stages (before and including day 14 after pollination), or 40% formalin, glacial acetic acid and 70% ethyl alcohol (FAA) in proportions 10:5:85 (Berlyn and Miksche 1976) at older stages for at least 48 hours, and then washed in 50% ethyl alcohol before dehydration. Johansen's (1940) ethyl alcohol/tertiary butyl alcohol (TBA) method was used for dehydration. Afterwards, the materials were processed by the paraffin technique. Serial longitudinal and cross sections were stained with 1% safranin solution for 24–48 hours and counterstained with 0.5% fast green for 5 seconds (Johansen 1940).

Results

Flower, Ovary and Ovule

Sandersonia flowers are bisexual with six stamens in two whorls. The ovary is superior, tricarpellate, syncarpous, and trilocular with axile placentation. The ovary is deeply trisulcate as the carpels are joined only along their inner margins (Figure 1). There are three segregated styles with superior stigmas. Each carpel contains numerous ovules (Figure 1).

The ovules are anatropous, crassinucellate and bitegmic (Figure 2). The micropyle is formed by the inner integument (Figure 2). The inner integument is biseriate except in the micropyle region, where more cell layers are present. The outer integument is mostly 4–5-seriate (Figure 2) and is not formed at the raphal side, only at the anti-raphe. Later the outer integument becomes a hood-shaped envelope. An obturator is present and the epidermal cells of the obturator and funicle are stained much more densely that those of the outer integument. A nucellar cap is located at the micropylar region and persists till the globular embryo stage (about 14 DAP). A well developed bowl-like hypostase is conspicuous in the chalazal region and does not disappear until about 42 DAP. A vascular bundle passes through the strophiole and terminates at the base of the hypostase.

In a mature ovule of *Sandersonia* the exostome is an inverted Y-shaped, transverse slit with a middle notch (Figure 2). Both outer and inner integuments form a micropyle, due to the outer integument overgrowing the inner one (Figure 2). An obturator is present on the concave side of the funiculus (Figure 2).

Ovule growth

Ovule extension over the period between pollination and seed maturity is plotted in Figure 3. Mean ovule diameter plotted against time results in a sigmoidal curve. There is no obvious growth of the ovule before the zygote starts the first division (the lag phase of the sigmoidal growth curve), with mean ovule diameter increasing from 0.39 to 0.48mm between 0 and 8 DAP (when the exponential growth phase begins) (Figure 3). During this period, double fertilisation occurs (not observed in this study), and then both the zygote and the primary endosperm nucleus are ready to start their divisions. As both the zygote and the primary endosperm nucleus begin their first divisions, rapid enlargement of the embryo sac occurs, as indicated by rapid growth of the ovule (Figure 3). Such enlargement is continuous and rapid until the embryo sac becomes fully cellular. After cellularisation of the endosperm, there is a slight increase in ovule diameter and the embryo becomes an elongate spheroid through the distal end elongating to form the cotyledonary initial (28 DAP). Beyond 28 DAP, the endosperm cells gradually accumulate storage materials and become hardened (thickening of the cell walls), which probably restricts further growth of the ovule. When the embryo develops into maturity at about 49–56 DAP, the ovule decreases in size (the mean diameter is about 2.34mm) through desiccation. At this time, the embryo is linear in shape and has a prominent radicle, a small embryonic axis and a cotyledon.

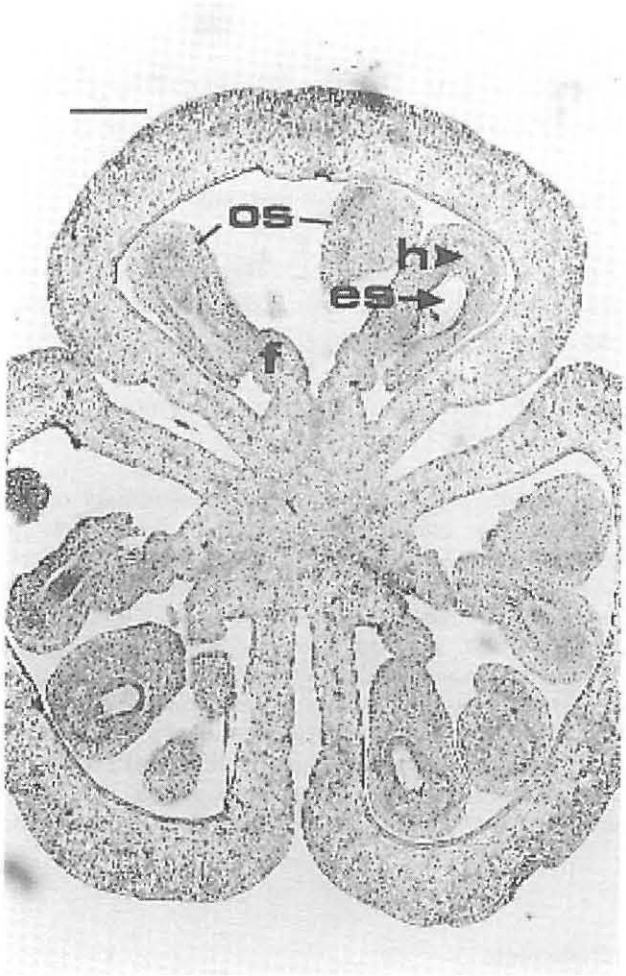

Figure 1: Transverse section of ovary at 1 DAP. The bar represents 1mm. os = ovules; es = embryo sac; h = hypostase; f = funiculus. Scale = 225µm

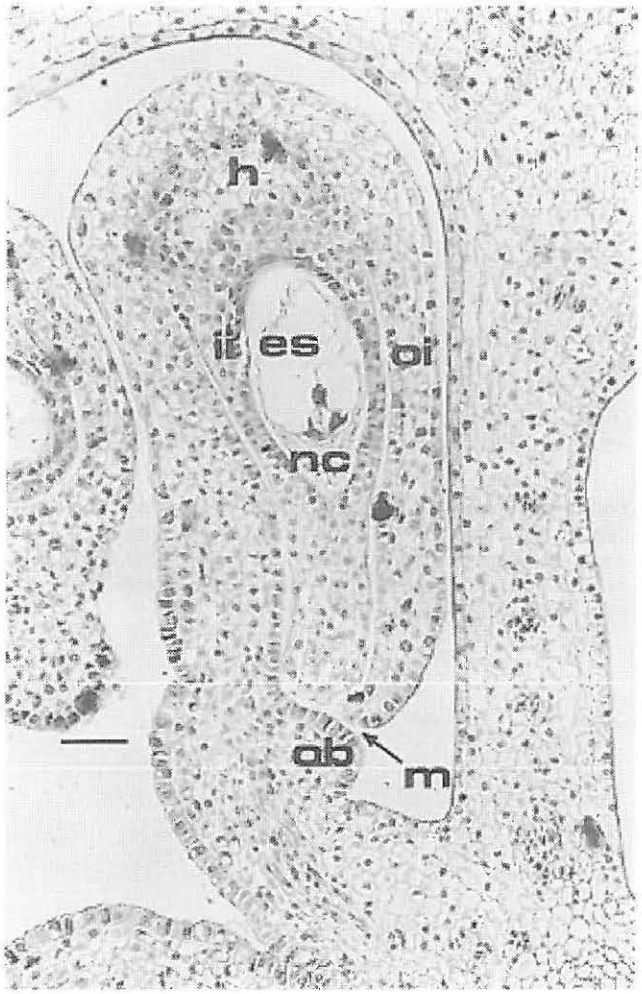

Figure 2: Longitudinal section of anatropous ovule at 1 DAP with micropyle (in outer integument region), obturator and hypostase. oi = outer integument; ii = inner integument; ob = obturator; h = hypostase; nc = nucellar cap; es = embryo sac; m = micropyle. Scale = 65µm

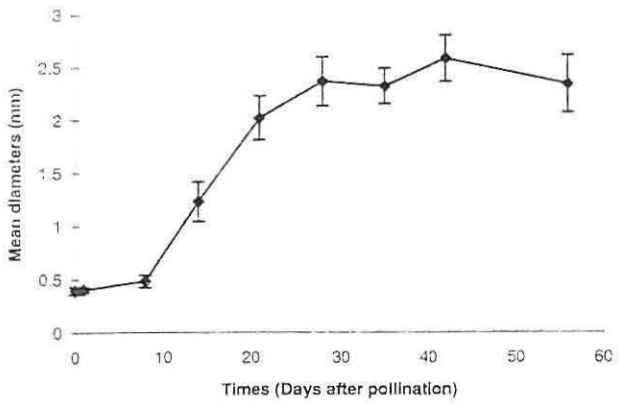

Figure 3: Mean ovule diameter during seed development of *Sandersonia*. The values are the mean diameter of 60 ovules ± mean standard deviation

Embryo Sac

The synergids appeared to be triangular in shape and to have densely staining cytoplasm without vacuoles (Figure 4). Both synergids disappear before the first division of the zygote. The egg cell is nearly the same size as the synergids, has a less dense cytoplasm and one to several vacuoles (Figure 4). After pollination, the two polar nuclei are in close contact and about 7 days after pollination (DAP), they fuse to form the secondary nucleus. The antipodal cells are located at the chalazal end of the embryo sac and after fertilisation, they enlarge (Figure 5) and often degenerate before the initiation of endosperm cellularisation.

Development of Endosperm

Endosperm development is of the nuclear type. The primary endosperm nucleus undergoes divisions soon after its formation. After several divisions, most of the coenocytic nuclear endosperm and cytoplasm is situated in the chalazal end of the embryo sac close to the hypostase. Small num-

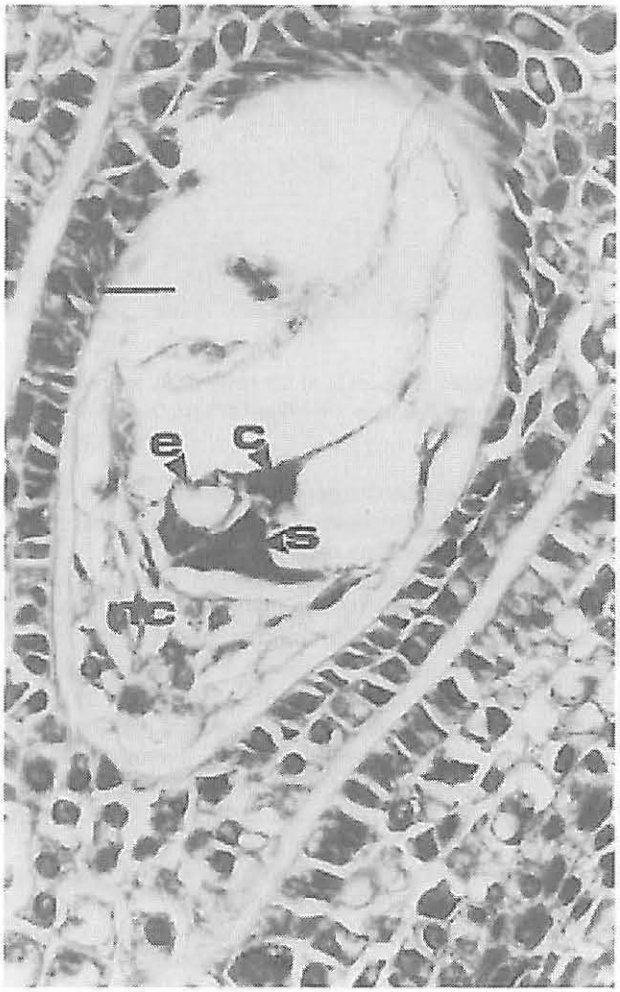

Figure 4: Embryo sac at 1 DAP. s = synergid; e = egg cell; c = central cell; nc = nucellar cap. Scale = 40µm

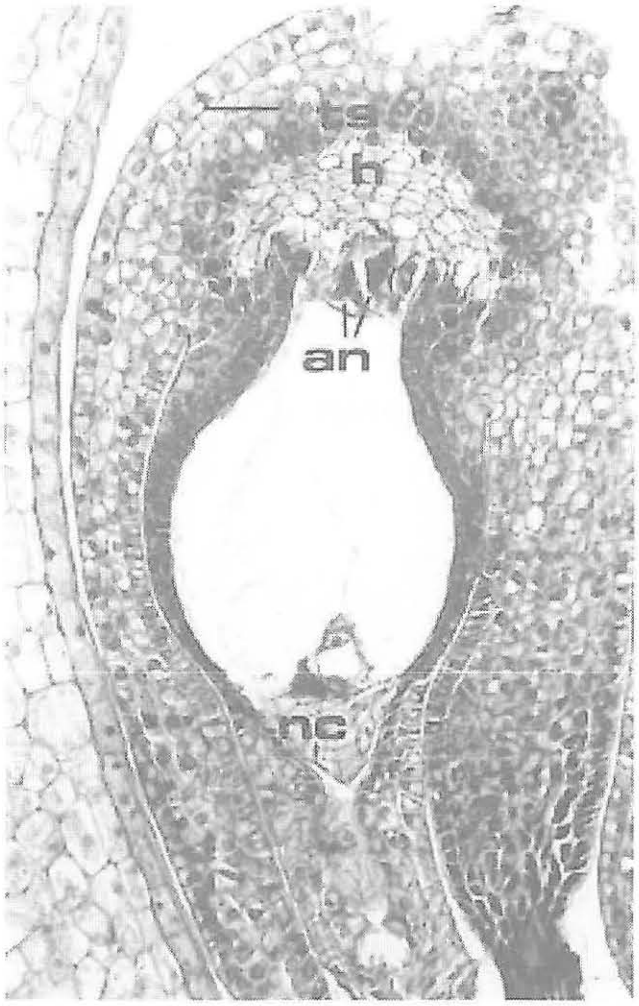

Figure 5: Enlarged antipodals at 10 DAP. an = antipodals; h = hypostase; ts = transfer cells; nc = nucellar cap. Scale = 50μm

bers of free nuclei of endosperm are also distributed in a thin layer of peripheral cytoplasm. The remainder of the embryo sac is occupied by a large central vacuole.

Endosperm cell wall formation begins at about 14 DAP during the early stage of embryogenesis. Wall formation is initiated at the chalazal end and the edges of the embryo sac, and extends inward and toward the micropylar end. As the process of wall formation proceeds, a band of cellular endosperm several cells thick forms around the edge of the embryo sac and the central vacuole decreases in size (Figure 6). Finally, at about 21 DAP, the whole area of the embryo sac from chalazal to micropylar region has become filled with cellular endosperm (Figure 7).

In a mature seed, endosperm cells are well developed and possess thickened walls. At later embryo stages, many small bodies are present in the cytoplasm of the endosperm cells (Figure 8) but the iodine test for starch did not reveal the presence of starch granules. These small bodies are also found in the cells of the ovary wall, outer integument and suspensor.

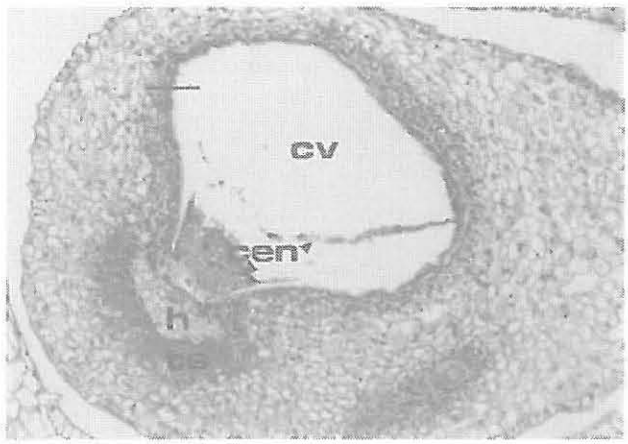

Figure 6: Longitudinal section of embryo sac showing the coenocytic nuclear endosperm and cytoplasm situated in the chalazal end and peripheral zone of the embryo sac at 14 DAP. h = hypostase, cv = central vacuole; cen = coenocytic nuclear endosperm; ts = transfer cells. Scale = 100μm

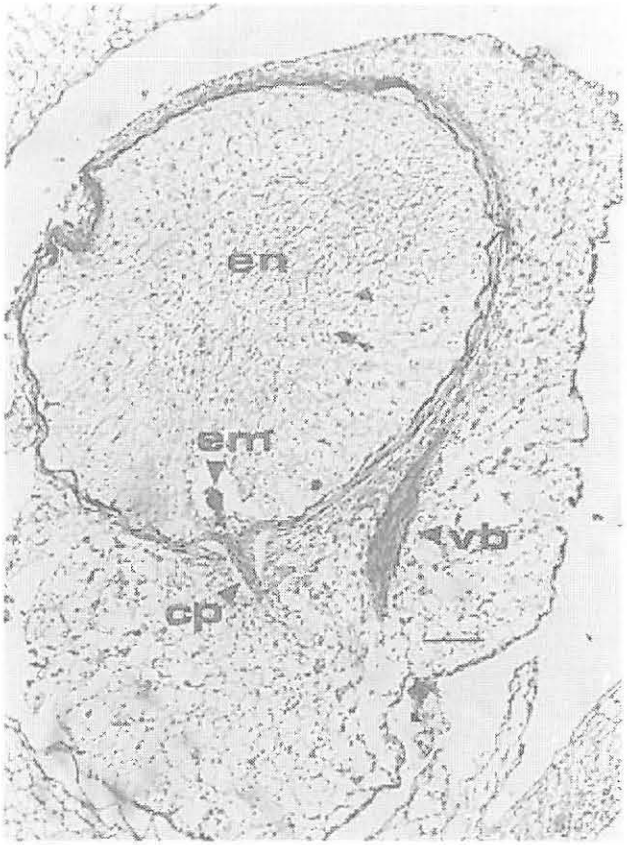

Figure 7: Completely cellularised endosperm at 21 DAP. em = embryo, en = endosperm; vb = vascular bundle; cp = cylindrical protuberance. Scale = 80μm

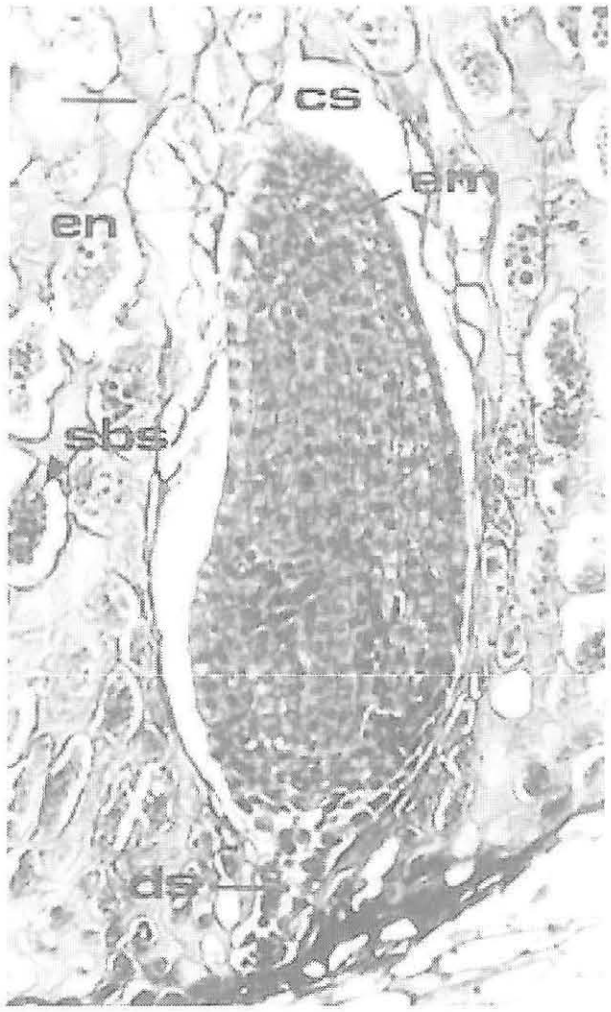

Figure 8: Linear embryo with a degenerating suspensor surrounded by a clear space and endosperm cells at 49 DAP. em = embryo proper; ds = degenerating suspensor; en = endosperm; cs = clear space; sbs = small bodies. Scale = 75µm

Development of Embryo

The zygote begins division at about 9 DAP. The first division of the zygote is transverse resulting in a smaller apical and a larger basal cell. This is followed by another transverse division of the basal cell, so that the three-celled embryo consists of an apical cell and two basal cells (Figure 9). The proembryo at 14 DAP has a 4–8 celled embryo proper and an 8–9 celled suspensor. About 18–21 DAP, the embryo develops into the late globular stage (Figure 10). The cotyledonary primordium appears at about 28 DAP, giving the embryo its distinctive ovoid shape (Figure 11). The growing point of the shoot is apparent on the side of the embryo about 35–42 DAP (Figure 12). The embryo in a mature seed (56 DAP) shows a prominent radicle, a small embryonic axis, shoot apex and a large cotyledon (Figure 13).

The suspensor, which is produced by a series of divisions of the basal cell, is observed from 14 DAP and remains to 49

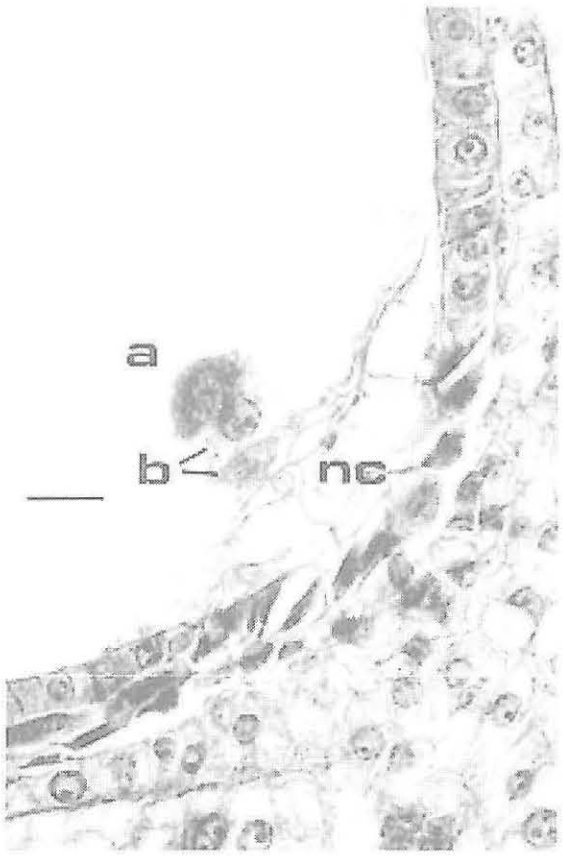

Figure 9: Three-celled proembryo at 9 DAP. a = apical cell; b = basal cells; nc = nucellar cap. Scale = 20µm

DAP. It comprises up to nine tiers of cells and a large basal cell (Figures 10 and 11).

Development of Seed Coat

At anthesis (day 0) the outer integument consists of 4–5 layers of parenchyma, and the inner one contains 2 layers (Figure 2). The differentiation of the seed coat begins about 12 DAP. At this time, the seed is about 1.0mm in diameter (Figure 3); the cells of the outer integument are arranged in an organised fashion and have nuclei and large vacuoles; the inner integument cells are smaller and contain a dense cytoplasm with small vacuoles. At approximately 14 DAP, the cells of the outer integument become enlarged and show more vacuolation, while the inner ones are crushed and begin lignifying (Figure 15). At 28 DAP, four types of cells can be recognised in the seed coat: (1) an epidermis consisting of one layer of cells, (2) several layers of large parenchyma cells which enlarge and lose their contents, (3) several layers of cells showing flattening and compression, and (4) a lignified layer which is derived from the crushed cells of the inner integument (Figure 15). By 42 DAP, the cells in (3) may degenerate or have become crushed with those in (4), and show a high degree of lignification (Figure 16). In the mature seed, these lignified cells develop into a mechanical barrier covering the endosperm (Figures 16 and 17).

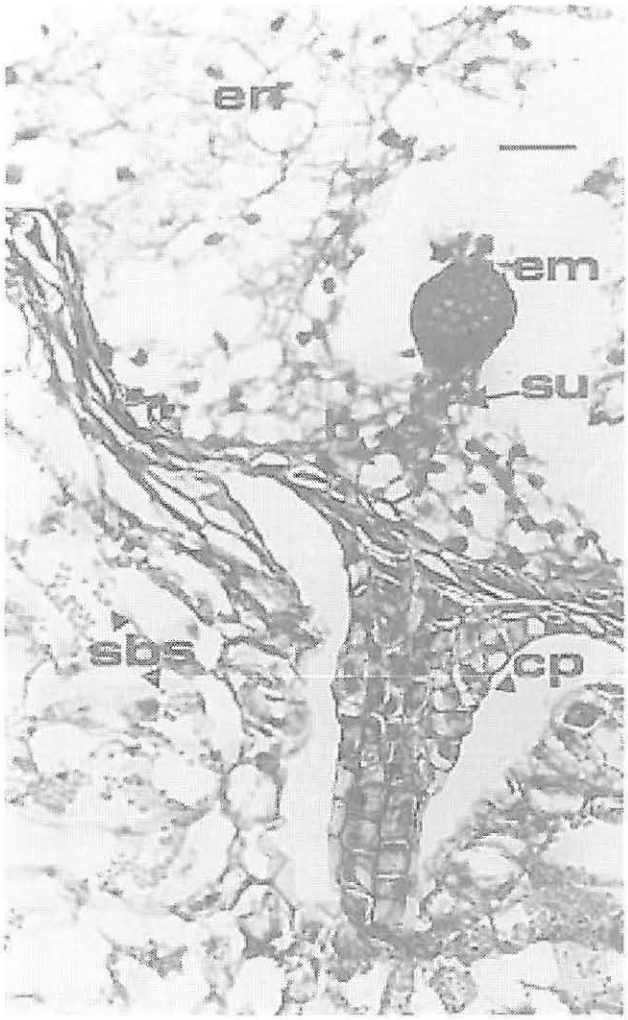

Figure 10: Late globular embryo surrounded by endosperm cells at 21 DAP. em = embryo; b = basal cell; su = suspensor; en = endosperm; cp = cylindrical protuberance; sbs = small bodies. Scale = 40μm

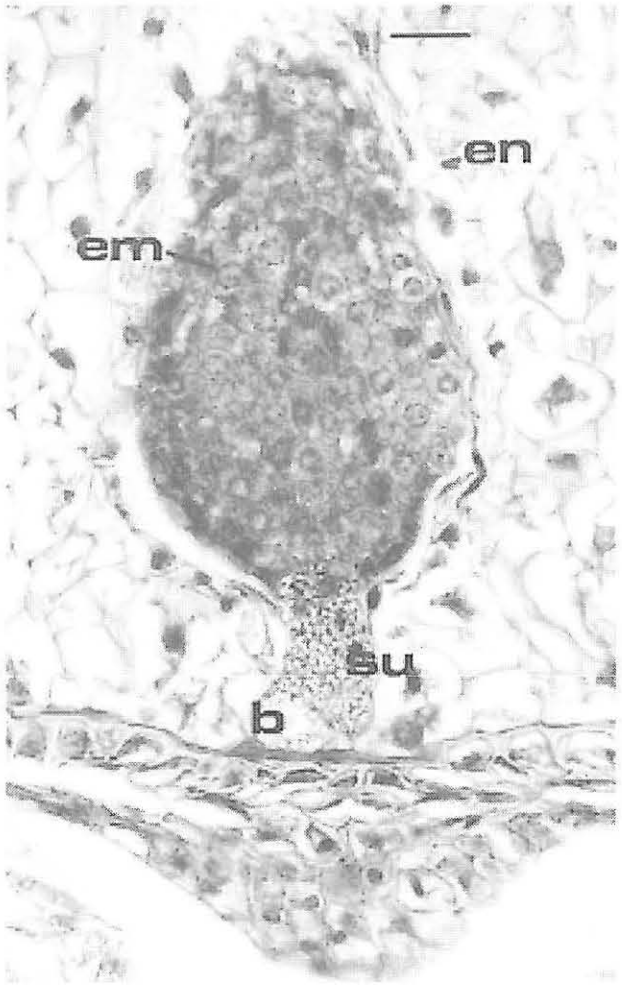

Figure 11: Elongated spheroidal embryo with a suspensor at 28 DAP. em = embryo; b = basal cell; su = suspensor, en = endosperm; sbs = small bodies. Scale = 25μm

Seed Structure

The mature seed is globose with a strophiole around the micropyle (Figure 17) and is dark brown in colour. Diameter varies from 2.07mm to 2.61mm (Figure 3) and the surface is rough. The seed coat of a mature seed is comprised of three layers: the epidermis, the subepidermal parenchyma (middle layer), and the lignified layer (Figure 16). Both epidermis and subepidermis come from the outer integument. The lignified layer is derived from both outer and inner or only inner integuments, which is stained red in colour by safranin suggesting lignification (Johansen 1940). At the micropylar end the outer integument increases in thickness forming the strophiole (Figure 17). The embryo is linear and very small, only 0.8mm in length and 0.25mm in diameter and embedded in the endosperm (Figure 13). The mature embryo shows a prominent radicle, a small embryonic axis, shoot apex and a large cotyledon (Figure 13). The endosperm constitutes most of the seed volume (Figures 7 and 17). The hilum develops in the side of the seed and may form from the chalaza shifting in the raphal direction.

Embryo and endosperm development in *Sandersonia* are not synchronous among the ovules from an individual ovary. Specimens collected at any one time contain embryos of varying sizes and endosperm of varying stage. Specimens collected during any given week may contain embryos further developed than some taken the following week. However, a general development scheme can be constructed by observing many randomly collected specimens.

Discussion

Ovary and Ovule

The results of the present study confirm those of Sterling (1975) that the ovary of *Sandersonia* has a tricarpellate form. Each carpel contains numerous ovules which are anatropous, bitegmic and each ovule has an obturator on the concave side of the funiculus. However, the study also shows that there are open sutures which extend inward in

Figure 12: Longitudinal section of linear embryo at 42 DAP. en = endosperm; cot = cotyledon; sa = shoot apex; cs = clear space. Scale = 50μm

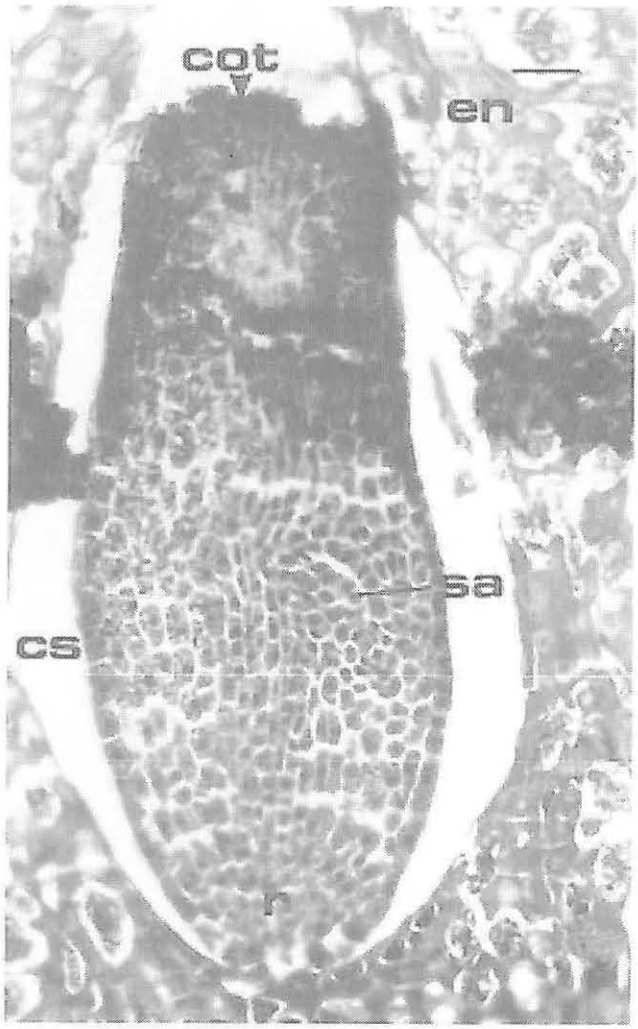

Figure 13: Linear embryo in a mature seed at 56 DAP. cot = cotyledon; sa = shoot apex; ea = embryonic axis; r = prominent radicle; cs = clear space. Scale = 30μm

the ovary along the septal boundaries of the carpels, a well-developed, bowl-like hypostase below the embryo sac in the chalazal region and the ovule has a crassinucellate structure.

The hypostase is made up of a group nucellar cells which lose their cytoplasm and nuclei, and are thick-walled. These cells are surrounded by several layers of cells which are stained much more densely than those of the integument cells (Figures 5 and 6) and may be transfer cells. The hypostase is known in many families, e.g. Amaryllidaceae, Cyperaceae, Liliaceae, Zingiberaceae, Anacardiaceae, Bixaceae, Euphorbiaceae, Lauraceae, Sapindaceae, Theaceae (Bouman 1984). Many functions have been attributed to the hypostase. It might be found only in the mature ovule, and in certain stages of seed development, or it may persist into the mature seed (Bouman 1984). Based on its structure, its location (close to the end of the vascular bundle) and because it is surrounded by transfer cells, it seems likely that the hypostase in *Sandersonia* ovules may connect the vascular supply with the embryo sac and facilitate transport of nutritional material.

Development of Endosperm

The present study shows that endosperm development in *Sandersonia* is of the nuclear type. The cellularisation of endosperm commences at the early globular stage and terminates at the late globular stage. That the differentiation of cellular endosperm began in the early globular stage of embryo development was also reported in *Helianthus annuus* (Newcomb 1973). Various researchers have described different patterns of endosperm wall formation. For instance it may start at the micropylar end of the embryo sac and progress toward the chalazal end (Shoemaker 1905, Newcomb 1973, Newcomb 1978) or it may occur simultaneously in all regions (Frye 1902). However, endosperm wall formation in *Sandersonia* starts at the chalazal end and proceeds micropylarly and centripetally.

It is generally accepted that the endosperm is a source of metabolites for the developing embryo. After the elongated spheroidal stage of embryo development (about 28 DAP) a

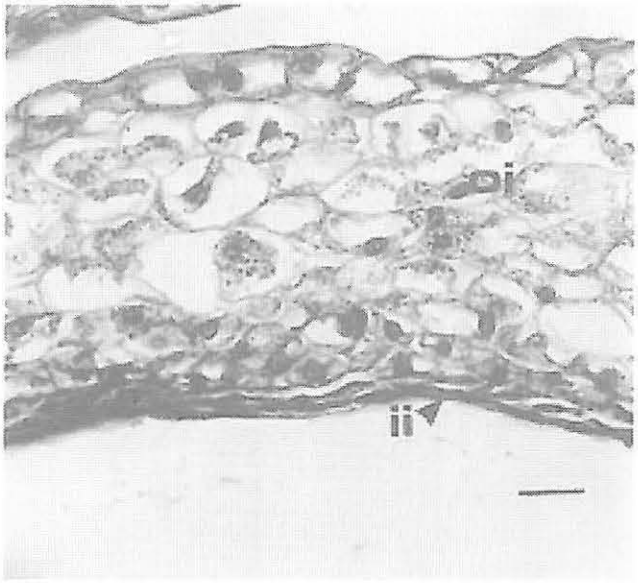

Figure 14: Developing seed coat at 14 DAP. oi = outer integument, ii = inner integument. Scale = 25μm

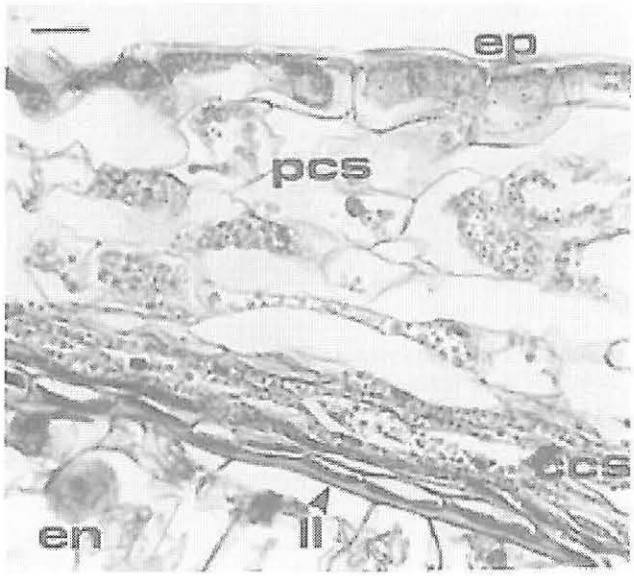

Figure 15: Seed coat at 28 DAP with four types of cells. en = endosperm; ep = epidermis; pcs = parenchyma cells; ccs = compressed cells; ll = lignified layer. Scale = 25μm

clear area appears in the endosperm adjacent to the embryo. Such an area has been postulated as representing the remains of digested endosperm (Newcomb 1973), therefore it seems reasonable that the embryo of *Sandersonia* is at least using the endosperm after the elongated spheroidal stage.

The small bodies in the cells of the ovary wall, outer integument and the suspensor are likely to be lipid bodies. These bodies have previously been described in the

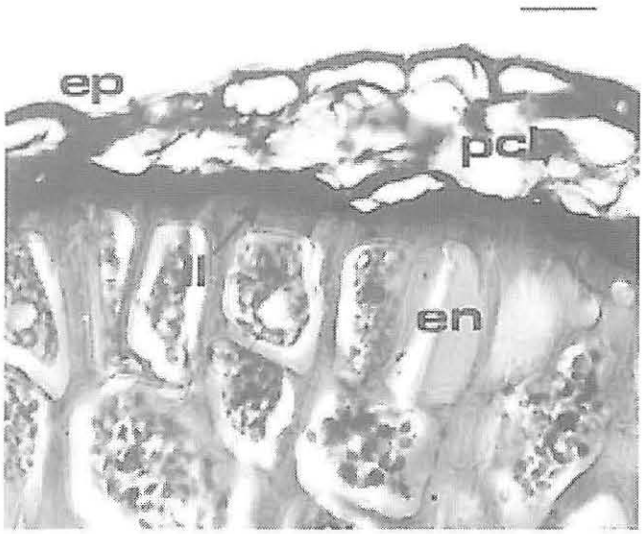

Figure 16: Seed coat at maturity stage (56 DAP). ep = epidermis; pcl = parenchyma cell layer; ll = lignified layer; en = endosperm. Scale = 35μm

endosperms of members of the Colchicaceae (Dahlgren *et al.* 1985).

Development of Embryo

Veyret (1974) indicated different embryo types according to the early cell division pattern of the embryo: Six main types of embryogeny have been described by Schnarf as well as Johansen (cited in Natesh and Rau 1984) based on the transverse division of the zygote and the respective contributions of the two daughter cells to subsequent formation of the embryo and its suspensor. In *Sandersonia*, the first division of the zygote is transverse resulting in a smaller apical and a larger basal cell. The basal cell generally divides first, into two cells. These results are similar to those in *Lilium parryi* (Liliaceae) described by Johansen (1950). The following divisions could not be determined in this study, and hence developing *Sandersonia* embryos can not be classified to any particular type of embryogeny. However, the Caryophyllad and Piperad types can be eliminated since the basal cell never divides again in the former and the first division of zygote is vertical in the latter (cited in Natesh and Rau 1984).

Embryo development of *Sandersonia* passes through the following stages: the early globular (about 14 DAP), the late globular (about 21 DAP), the elongated spheroidal (about 28 DAP), and the linear embryo (after 35 DAP). The mature embryo has little differentiation, but a radicle, a small embryonic axis, shoot apex and a cotyledon can be recognised (Figure 13). The development of embryos in *Allium fistulosum* L. is of the Asterad type (Xiang-Yuan 1987) and its pattern of embryo development is very similar to those in *Sandersonia* till the elongated spheroidal stage. However, embryo development in *A. fistulosum* L. is faster than that in *Sandersonia* and results in a well-developed, curved embryo.

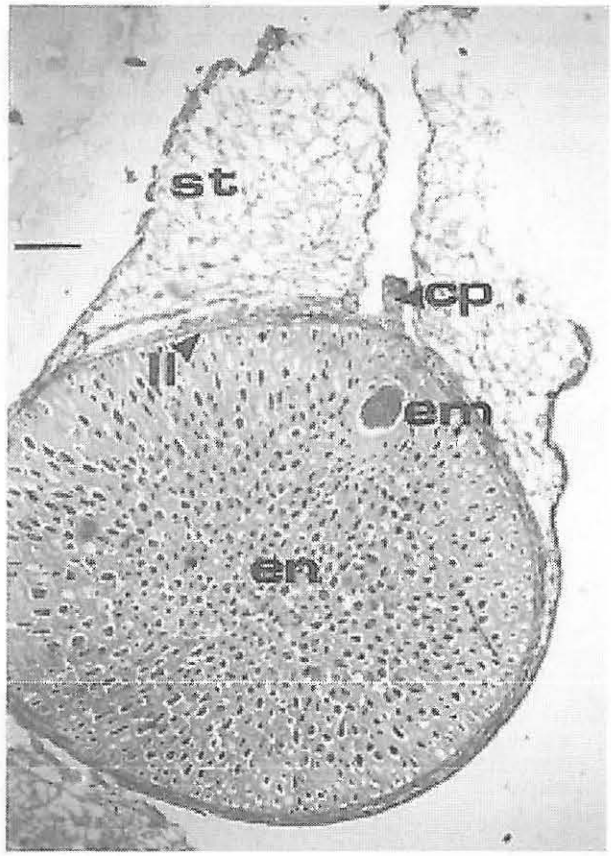

Figure 17: Longitudinal section of a dry seed. cp = cylindrical protruberance; em = embryo; en = endosperm; ll = lignified layer; st = strophiole. Scale = 250µm

A well-developed suspensor was found in the *Sandersonia* embryo from about 14 DAP to 49 DAP. It contains a large basal cell and a number of suspensor cells arranged in one or two tiers under the embryo proper. *A. fistulosum* L. has a short suspensor comprised of two tiers of 4 cells each which remains to the spheroidal embryo stage (Xiang-Yuan 1987). Similar suspensor structures are also found in some species of Liliaceae. For example, a suspensor of five or more cells in *Calochortus* remains more or less intact when the embryo is mature (Johansen 1950); a well-developed filamentous suspensor is found in *Pushkinia scilloides* (Johansen 1950); and *Anthericum ramosum* possesses a suspensor in the form of several superposed flattened cells (Johansen 1950). In addition to pushing the growing embryo into the embryo sac, the suspensor is believed to play an important role during early embryo development. It has been shown in *Phaseolus* that the suspensor is an important uptake site for the developing embryo (Yeung 1980) and is a major site for gibberellin synthesis (Picciarelli and Alpi 1986). In *Calypso*, the basal cell of the suspensor enlarges rapidly (Yeung and Law 1992). This rapid expansion presses the cell tightly against the integuments of the maternal tissues. It is reasonable to suppose that the suspensor in *Sandersonia* may play an important role during early embryo development, because: (1) the two synergids disappear before the first division of the zygote; (2) the suspensor is present until the embryo is nearly mature; (3) the basal cell is closely attached to the embryo sac wall at the micropylar end during the whole period of embryo development; and (4) small storage bodies which are present in mature endosperm cells are also found both in the suspensor cells and the basal cell.

Seed Coat Development and Seed Structure

Results from this study suggest that no or few cell divisions occur in the integumentary cells after fertilisation, but that the seed coat is formed through the elongation and differentiation of integumentary cells. Integuments with mainly anticlinal divisions and no increase in the number of layers are called non-multiplicative integuments (Corner 1976), and generally have a simple structure which may be two- or three- or paucilayered. The seed coat in *Sandersonia* derives from the two integuments. The inner integument has two layers of cells and develops before the outer one does. At maturity, the cells of the inner integument are completely crushed and lignified, forming a mechanical barrier surrounding the endosperm tissue. The outer integument develops 2 days later than the inner one. It is non-multiplicative and reduced in thickness and forms an outer epidermis (one layer of cells) and a subepidermal parenchyma layer (several layers of cells). The innermost layer of outer integument cells may degenerate or fuse with inner integument cells to form the lignified layer.

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